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Dissecting a biodiversity hotspot: the importance of environmentally marginal habitats in the Atlantic Forest Domain of South America

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Running head: Stress gradients across the Atlantic Forest Hotspot

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ABSTRACT

Aim: We aimed to assess the contribution of marginal habitats to the tree species richness of the *Mata Atlântica* (Atlantic Forest) biodiversity hotspot. In addition, we aimed to determine which environmental factors drive the occurrence and distribution of these marginal habitats.

Location: The whole extension of the South American Atlantic Forest Domain plus forest intrusions into the neighbouring Cerrado and Pampa Domains, which comprises rain forests ('core' habitat) and five marginal habitats, namely high elevation forests, rock outcrop dwarf-forests, riverine forests, semideciduous forests and *restinga* (coastal white-sand woodlands).

Methods: We compiled a dataset containing 366,875 occurrence records of 4,431 tree species from 1,753 site-checklists, which were *a priori* classified into ten main vegetation types. We then performed ordination analyses of the species-by-site matrix to assess the floristic consistency of this classification. In order to assess the relative contribution of environmental predictors to the community turnover, we produced models using 26 climate and substrate-related variables as environmental predictors.

Results: Ordination diagrams supported the floristic segregation of vegetation types, with those considered as marginal habitats placed at the extremes of ordination axes. These marginal habitats are associated with the harshest extremes of five limiting factors: temperature seasonality (high elevation and subtropical riverine forests), flammability (rock outcrop dwarf-forests), high salinity (*restinga*), water deficit severity (semideciduous forests) and waterlogged soils (tropical riverine forests). Importantly, 45% of all species endemic to the Atlantic Domain only occur in

marginal habitats.

Main conclusions: Our results showed the key role of the poorly protected marginal habitats in contributing to the high species richness of the Atlantic Domain. Various types of environmental harshness operate as environmental filters determining the distribution of the Atlantic Domain habitats. Our findings also stressed the importance of fire, a previously neglected environmental factor.

Keywords: campo rupestre, climate, conservation assessment, flammability, rain forests, restinga, stress gradients, variation partitioning

(A) INTRODUCTION

The Atlantic Forest of South America, or the *Mata Atlântica* as it is known in Brazil where it largely occurs, stretches for over 3,500km across equatorial, tropical and subtropical latitudes, and is renowned worldwide for being one of the 35 biodiversity hotspots for conservation prioritisation (Myers *et al.*, 2000). Its importance is also demonstrated by its designation as one of the five primary vegetation 'Domains' of Brazil (IBGE, 1993; Ab'Sáber, 2003), the others being the Caatinga, Cerrado, Pampa and Amazon Domains. The Atlantic Forest Domain (hereafter Atlantic Domain) borders all the other Domains except for the Amazon. The prevailing land cover of these bordering Domains are semi-arid thorn woodlands in the Caatinga, woody savannas in the Cerrado and prairies in the Pampa. Species from rain forests, the habitat that originally prevailed in the Atlantic Domain, become a minor component of the landscape in these neighbouring Domains, and they are only found in riverine or high elevation forest enclaves.

Environmental restriction to the establishment of the rain forest habitat is certainly operating at the boundaries of the Atlantic Domain. In a seminal paper, Scarano (2009) proposed a list of five key factors limiting the occurrence and distribution of rain forest species in the Atlantic Domain, which at its harshest extremes give rise to distinct habitats (one for each factor), referred to as marginal habitats. Therefore, the rain forest is placed by Scarano (2009) as the 'core' expression of the Atlantic Domain, where deep shade plays the chief role as a limiting factor for competing plants. The five marginal habitats are high elevation forests, rock outcrop dwarf-forests, riverine forests, seasonally dry forests and

restinga (coastal white-sand woodlands). Most of these marginal habitats have a relatively high density of trees and can be considered forests, albeit not as well developed structurally as rain forests. High elevation forests are primarily associated with frost, with secondary limitation imposed by drought (leeward rain-shadow) and high light intensity. Cloud forests and *Araucaria*-dominated forests are the main vegetation types of highlands in the Atlantic Domain. Rock outcrop dwarf-forests, found at lower elevations (and even at the seashore), are primarily limited by the paucity, or even lack, of soil and related poor water retention. Meanwhile, riverine forests are associated with waterlogging on lowland plains and riverbeds. Seasonally dry forests (either deciduous or semideciduous) replace rain forests where seasonal rainfall regimes bring regular periods of drought. Finally, environmental harshness for *restinga* is primarily associated with salinity, with secondary limitations imposed by drought and low fertility in mineral nutrients (Scarano, 2009) (Fig. 1).

Within limited areas, some studies have confirmed the leading role of Scarano's limiting factors as distribution filters for plants. These studies addressed tree species composition for particular sectors of the Atlantic Domain, such as the South-east (Oliveira-Filho & Fontes, 2000; Eisenlohr & Oliveira-Filho, 2015), the subtropical South (Oliveira-Filho *et al*., 2015) and the highly biodiverse central region in eastern Bahia state, northeastern Brazil (Saiter *et al*., 2016). However, the whole of the Atlantic Domain has only been investigated for epiphytic angiosperms (Menini-Neto *et al.*, 2016). Also, the Atlantic Domain is affected by fire in much of its distribution (Archibald *et al.*, 2013), though to a less extent than in surrounding Domains, such as in central (Cerrado woody savannas) and southern Brazil (Pampa prairies). Nevertheless, the potential effect of fire in limiting plant species distribution across the Atlantic Domain is yet to be investigated. Here we bring together a novel

and comprehensive dataset assembled to date on the composition of tree communities across the whole Domain (c. 2,000 community surveys across core and marginal habitats, with > 1,000 sites representing surveys not used in the aforementioned studies), combined with environmental data, focusing on testing Scarano's proposed limiting variables as well as factors that were neglected in previous studies (e.g., fire).

Besides the importance for community ecology, understanding the degree to which limiting factors drive community differentiation is inherently relevant for conservation. The Atlantic Domain houses c.18,000 plant species (REFLORA, 2017), but the current high levels of fragmentation and the continuous habitat loss throughout the Domain has raised several concerns in the scientific community (Galindo-Leal *et al.,* 2003; Tabarelli *et al.*, 2004; 2005; Joly *et al.*, 2014). Therefore, we believe the time is ripe for studies aiming to test the overall importance of environmental conditions in controlling the occurrence and distribution of plant species across the whole extent of the Atlantic Domain and, more importantly, across both its core and marginal habitats.

We addressed the following questions: (i) are the patterns of tree species distribution across the Atlantic Domain, and its intrusions into neighbouring Domains, limited by factors associated with water deficit (via both soil depth and dry season), water excess (via waterlogging), frosts (via low temperature), and soil salinity? If previously unrecognized environmental conditions are the main factors explaining the patterns of tree species distribution, Scarano's (2009) limiting factors should account for a small proportion of the variation in community composition explained by environmental factors; (ii) are these limiting factors leading to floristically distinct marginal habitats? If the community composition of the marginal habitats is simply a

nested subset of the more diverse Atlantic Domain rain forest, species turnover should account for a small fraction of the dissimilarity between rain forest and marginal habitats; and (iii) what is the contribution of these marginal habitats to the overall high species richness of the Atlantic Domain?

(A) METHODS

(B) Study area

The Atlantic Forest, designated as one of the five phytogeographical 'Domains' of Brazil (IBGE, 1993; Ab'Sáber, 2000), occurs primarily along the Atlantic coast and is bordered by the Pampa Domain (woody prairies) of southern Brazil and by the 'dry diagonal', a corridor that includes three other phytogeographical Domains: Caatinga (semi-arid thorn woodlands) of northeastern Brazil, Cerrado (woody savannas) of central Brazil, and Chaco (semi-arid thorn woodlands) of Paraguay–Argentina–Bolivia (IBGE, 1993, Prado & Gibbs 1993, Neves *et al*. 2015). The South American Atlantic Forest Domain (hereafter Atlantic Domain) has a history of controversies over its geographical circumscription and associated terminology. The controversy may be summarized by three main concepts of Atlantic Domain habitats: the *sensu stricto*, *sensu lato* and *sensu latissimo* concepts (Oliveira-Filho *et al*., 2006). The first, and most restrictive concept, includes only the tracts of rain forests that occur as a narrow band along the coast (<100 km wide and up to 2500 m elevation) and stretches all through the Domain, though with two main interruptions, the São Francisco Gap and Campos dos Goytacazes Gap. The former has a semi-arid nucleus at the mouth of the São Francisco River (~10°30'S), and the

latter is a seasonally dry region extending from southern Espírito Santo to northern Rio de Janeiro (RJ) States, with its driest extreme at Cabo Frio/RJ (~22°50'S).

The *sensu lato* concept of Atlantic Domain habitats, which is currently prevalent, includes other habitats adjacent to rain forests, such as the much more extensive semideciduous forests that cover increasingly larger areas towards the south and become wide enough to reach eastern Paraguay and north-eastern Argentina. *Araucaria*-dominated forests are also a very important component of the *sensu lato* concept, followed by coastal woodlands on white-sand substrates (termed *restingas*) and three highland dwarf-forests: rocky cloud dwarf-forests, rocky semideciduous dwarf-forests and rocky highland savannas (termed *campos rupestres*).

The *sensu latissimo* concept of Atlantic Domain habitats proposed by Oliveira-Filho *et al*. (2006) surpasses the geographical limits of the Atlantic Domain to include riverine and deciduous forest tracts occurring in the neighbouring Domains as a secondary component of the landscape, though with a typically Atlantic Domain flora. In the present contribution we adopt this concept because it allows a more complete inclusion of marginal habitats. However, deciduous forests found in the Cerrado and Pampa Domains, one of the forest types in the *sensu lato* concept (IBGE, 1993), were not included in this contribution because previous studies (e.g. Oliveira-Filho *et al*., 2006; Eisenlohr & Oliveira-Filho, 2015) have demonstrated that their flora is distinct and more closely related to that of semi-arid woodlands (e.g. in the Caatinga Domain).

(B) Dataset

We extracted the dataset from the NeoTropTree (NTT) database (http://prof.icb.ufmg.br/treeatlan), which consists of tree species checklists (trees defined here as freely standing woody plants >3 m in height) compiled for geo-referenced sites, extending from southern Florida (U.S.A.) and Mexico to Patagonia. NTT currently holds 5,126 sites/checklists, 14,878 woody plant species and 920,129 occurrence records. A site/checklist in NTT is defined by a single habitat, following the classification system proposed by Oliveira-Filho (2015), contained in a circular area with a 10-km diameter. Therefore, where two or more habitats co-occur in one 10-km area, there may be two geographically overlapping sites in the NTT database, each for a distinct habitat.

The data were originally compiled from an extensive survey of published and unpublished (e.g. PhD theses) literature, particularly those on woody plant community surveys and floristic inventories. Moreover, new species occurrence records obtained from both major herbaria and taxonomic monographs have been added to the checklists when they were collected within the 10-km diameter of the original NTT site and within the same habitat. All species and their occurrence records were checked regarding current taxonomic and geographical circumscriptions, as defined (in the present case) by the team of specialists responsible for the online projects *Flora do Brasil* and *Flora del Conosur* (available at http://floradobrasil.jbrj.gov.br/ and http://www.darwin.edu.ar/, respectively). NTT does not include, therefore, occurrence records with doubtful identification, location or habitat, nor sites with an indication of high anthropogenic disturbance. The latter is assessed by taking into account the information available in the studies that comprise the checklists, and by direct observation of site surface on Google Earth©. It also excludes checklists with low species richness (< 20 species), because this is

often due to low sampling/collecting efforts, which results in poor descriptive power.

This study used a subset of tree inventories from the NTT database, consisting of 328 rain forest sites and 1,425 sites representing the limiting environmental factors and marginal habitats proposed by Scarano (2009), namely seasonally dry (663 semideciduous forests), high elevation (193 *Araucaria*-dominated forests and 61 cloud forests), rock outcrops (49 rocky cloud dwarf-forests, 31 rocky semideciduous dwarf-forests and 41 *campos rupestres*), high salinity (181 restingas - with only forests and dwarf-forests of the mosaic included) and waterlogged soils (133 tropical riverine forests and 73 subtropical riverine forests. Note that marginal habitats associated with seasonal drought and high salinity are represented by one vegetation type, whereas high elevation, rock outcrops and waterlogged soils are represented by more than one vegetation type. The final species matrix contained presence/absence data for 4,431 tree species across 1,753 sites, with a total of 366,875 presences (see Fig. 2a-b).

The NTT database also included 26 environmental variables for all its sites, derived from multiple sources (at a 30 arc-second resolution; detailed below). The resolution used in this study was particularly appropriate (1 km^2) because all sites are more than 1 km distant from each other (only 124 out of 1,753 sites are less than 5 km distant from another site and the mean distance between all sites is > 1,000 km). Elevation at the NTT site centre was used as an integrative environmental variable. Mean annual temperature, mean daily temperature range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean annual precipitation, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality were obtained from WorldClim 1.4 data layers (Hijmans *et*

al., 2005). WorldClim monthly temperatures and precipitation were also interpolated to obtain values for 5-day intervals by applying sinusoidal functions centered at day 15 of each month. These functions yielded values for days 1, 5, 10, 20, 25 and 30, which were used to generate Walter's Climate Diagrams (Walter, 1985) and, thus, four additional variables: duration (days) and severity (days) of both the water deficit and water excess periods. Frost frequency (days) and cloud interception (mm) were obtained from interpolating known values as response variables (data obtained from 135 and 57 Brazilian Meteorological Stations measuring frost frequency and cloud interception, respectively) with elevation, latitude and the WorldClim layers as predicting variables. Potential evapotranspiration (mm) and the aridity index (annual precipitation/potential evapotranspiration) were obtained from Zomer *et al.* (2007, 2008).

Surface rockiness (% exposed rock), soil coarseness (% sand), soil fertility (% base saturation) and soil salinity (ds/m) were obtained from the Harmonized World Soil Database v 1.2 (available at http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/) and ranked afterwards by mid-class percentage. The use of classes was adopted to add robustness to the data because of the high local soil heterogeneity that makes raw figures unrealistic. Soil drainage classes were obtained following EMBRAPA's protocol (Santos *et al*., 2013), which combines soil type, texture and depth with landforms. Soil drainage classes, mean annual precipitation (Hijmans *et al.*, 2005) and the aforementioned indices of water deficit and excess were also combined to produce a hyperseasonality index. Grass coverage (%) was used as a proxy of fire return interval (i.e., frequency). Previous studies give support to grass coverage as a good proxy of fire frequency (Hoffmann *et al.*, 2012; Archibald *et al.*, 2013; Lehmann

et al., 2014), although further quantification of fire regime is clearly needed (c.f. Archibald *et al.*, 2013). Grass coverage was obtained by direct observation of site surface on Google Earth© images in five 100×100m areas, one at the central coordinates of the NTT site and four at 2.5 km away from it and towards the NE, SW, NW and SE.

Further details of NTT history, products and protocols can be found at http://prof.icb.ufmg.br/treeatlan.

(B) Analyses of community turnover

We first explored the patterns of floristic differentiation between rain forest and marginal habitats by performing non-metric multidimensional scaling (NMDS) (McCune & Grace, 2002). We then assessed the relative importance of turnover and nestedness to floristic differentiation between rain forest and each of the marginal habitats. This analysis was performed by first calculating Jaccard pairwise distances, which ranges from 0 (identical in community composition) to 1 (completely different in community composition). These pairwise distances are then decomposed into dissimilarity due to species turnover (i.e., only compositional changes) and dissimilarity due to differences in species richness. The latter is the difference between Jaccard distance and the dissimilarity due to species turnover (Baselga, 2010). The ordination and the dissimilarity partitioning analyses were conducted in the statistical packages vegan (Oksanen *et al.*, 2016) and betapart (Baselga & Orme, 2012), respectively, both in the R Statistical Environment (R Development Core Team, 2015).

We assessed whether Scarano's (2009) limiting factors are the key

environmental factors driving variation in community composition, and then explored the results visually by plotting the habitats in geographic or ordination (NMDS) space and then fitting the values of the most important environmental variables via generalized additive models (GAM) and generalized linear models (GLM), respectively. This routine follows methods similar to those proposed by Blanchet *et al.* (2008) and Legendre *et al.* (2012), which comprises (i) the exclusion of 300 singletons (species found at a single site), as they commonly increase the noise in most analyses without contributing information (Lepš & Šmilauer, 2003); (ii) the Hellinger transformation of the binary presence/absence data (Legendre & Gallagher, 2001), which reduces the effect of widespread species; (iii) the independent compilation of significant spatial and environmental variables through a forward selection method for redundancy analysis (RDA), after first checking that the respective global models were significant (Blanchet *et al*., 2008); (iv) an additional and progressive elimination of collinear variables based on their variance inflation factor (VIF) and ecological relevance, until maintaining only those with VIF < 4 (Quinn & Keough, 2002); and (v) an RDA-based partitioning of variation in community composition matrix due to environmental variables, spatial autocorrelation and their combined, statistically indistinguishable effects. As spatial variables, we used principal coordinates of neighbour matrices (PCNMs; Borcard *et al.* 2004), which represent the spatial structure of the sampling units at multiple spatial scales without considering any environmental variation (Borcard *et al.*, 1992; Legendre *et al.*, 2002; Borcard *et al.*, 2004). We tested the overall significance of the environmental fraction (controlled for spatial autocorrelation) by applying ANOVA permutation tests (999 permutations) for RDA (Peres-Neto *et al.*, 2006). The variable selection, variation partitioning, NMDS, GLM and GAM analyses were conducted

using the fields (Nychka *et al.*, 2015), spacemakeR (Dray *et al.*, 2010) and vegan (Oksanen *et al.*, 2016) packages in the R Statistical Environment (the variation partitioning script is available as supporting information). The maps were designed using the package maptools (Lewin-Koh & Bivand, 2012) in the R Statistical Environment.

We also calculated patch statistics to test whether floristic differentiation can be modulated by habitat quality (a proxy for anthropogenic effect). We used the PatchStat function - available in the SDMTools package (VanDerWal et al., 2014) in the R Statistical Environment - and identified configuration metrics of landscapes (e.g., patch area, edge perimeter) for 95% of our sites using the vegetation map of the Brazilian Atlantic Domain (http://mapas.sosma.org.br/). We found that the effect of habitat quality was negligible in explaining variation in tree community composition across rain forests and marginal habitats (see SI for further details).

(B) Conservation assessment

We assessed how well the floristic diversity is captured in our dataset by calculating the expected species accumulation curves for rain forest and marginal habitats, using sample-based rarefaction (Colwell *et al.*, 2012) with the 'specaccum' function in the statistical package vegan (Oksanen *et al.*, 2016). We also explored levels of endemism for Atlantic Domain habitats. We obtained the lists of endemic species from Reflora (http://floradobrasil.jbrj.gov.br), which is the most comprehensive study of the patterns of plant species richness and endemism for phytogeographical Domains in eastern South America. Afterwards, we conducted an assessment of the conservation status of the Atlantic Domain habitats by overlaying

344 the distribution of our 1,753 sites on to the coverage of protected areas across South
345 America. We used conservation units from the World Database on Protected Areas
346 (IUCN & UNEP - WCMC, www.protectedplanet.net) and *Cadastro Nacional de*
347 *Unidades de Conservação* (Ministério do Meio Ambiente - Brazil,
348 www.mapas.mma.gov.br). Species accumulation curves are provided for rain forest
349 and marginal habitats as SI (Figs. S1).

350 Lastly, we used the main environmental variables emerging from the
351 community turnover models to create site groups discriminating the marginal habitats
352 and then processed the species matrix following the procedure proposed by Tichý &
353 Chytrý (2006) to produce sets of diagnostic species, which are provided as
354 supporting information (Table S2). This procedure is particularly suitable to quantify
355 the fidelity of species to groups that have unequal sizes, i.e., different numbers of
356 sampling units, as is the case with our study. After the groups are equalized, a
357 coefficient of fidelity is calculated and the significance of each diagnostic species is
358 obtained with 999 Monte Carlo permutations.

359

360 **(A) RESULTS**

361

362 **(B) Floristic patterns**

363

364 The distribution of the sites in the ordination space yielded by NMDS (Fig. 3a-
365 b) largely segregated rain forests and marginal habitats. The ordination placed
366 'marginal' vegetation types at the extremes of the first three ordination axes. Axis 1
367 segregated, at negative scores, the shoreline-associated *restinga* and, at positive
368 scores, the vegetation types associated with low-temperature extremes of higher

369 elevations and latitudes further from the equator (*Araucaria*-dominated forests and
370 subtropical riverine forests). Axis 2 segregated, at positive scores, vegetation types
371 associated with rock outcrops (rocky cloud dwarf-forests, rocky semideciduous
372 dwarf-forests and *campos rupestres*). Axis 1 further segregated rock outcrop
373 vegetation types into warmer sites (rocky semideciduous dwarf-forests and *campos*
374 *rupestres*), at positive scores, and colder sites (rocky cloud dwarf-forests), at
375 negative scores. Axis 3 placed the habitat associated with seasonal drought
376 (semideciduous forests) at intermediate scores and the habitat associated with
377 waterlogged soils at positive scores (tropical riverine forests).

378 The floristic composition of marginal habitats is not simply a nested subset of
379 the more species rich rain forest. The turnover component accounts for most of the
380 floristic dissimilarity of each marginal habitat in relation to rain forests (Fig. 4).
381 Nestedness is higher than the turnover component in very few cases (i.e., few
382 marginal habitat sites are simply a subset of another rain forest site; see
383 semideciduous forest triangle in Fig. 4) More specifically, vegetation types
384 associated with rock outcrops (including *campos rupestre*) have the higher fraction of
385 dissimilarity attributed to turnover while *restinga* and subtropical riverine forest have
386 the lower fraction attributed to turnover.

387

388 **(B) Variation partitioning analyses**

389

390 The forward selection procedure retained 13 environmental variables in the
391 model to explain the variation in tree species composition (Table 1). In partitioning
392 the variation explained by the retained environmental and spatial predictors, we
393 found that the environmental fraction explained 27% of the variation, 5% of which

was independent of spatial autocorrelation ($P < 0.01$). The environmental predictors could not account for a spatially structured variation of 12% ($P < 0.01$), and 61% of the variation remained unexplained (see discussion for more details).

The harshest extremes of the retained environmental variables (Table 1) do lead to distinct habitats, treated here in the context of 'marginal' vegetation types. A north to south increase in temperature seasonality was congruent with a latitudinal gradient in community turnover, which represents the floristic differentiation of *Araucaria*-dominated forests and subtropical riverine forests (Figs. 2a and 3a) from all other vegetation types. Grass coverage, a proxy for fire frequency (see Methods), was congruent with the floristic differentiation of the vegetation types associated with rock outcrops (including *campos rupestres*) from all others vegetation types (Fig. 3a). Within the rock outcrop habitat, the frequency of frost was associated with the floristic differentiation of rocky cloud dwarf-forests from the other rocky vegetation types. Soil salinity was congruent with a coast to inland gradient in community turnover, which represents the floristic differentiation of *restinga* from all other vegetation types (Fig. 3a). Another coast to inland gradient is evident in the tropical section of the Atlantic Domain, where water deficit severity and mean annual precipitation, proxies for drought-stress, explained the floristic differentiation of everwet vegetation types, namely rain forest, cloud forests and rocky cloud dwarf-forests, from *campos rupestres*, semideciduous forests, rocky semideciduous dwarf-forests and tropical riverine forests (Figs. 2b and 3b). At the harshest extreme of the drought-stress gradient (Fig. 3b), water-related hyperseasonality (i.e. ranging from water shortage to soil waterlogging) segregates *campo rupestres* and tropical riverine forests from semideciduous forests. These factors represent the seven most explanatory environmental variables (Table 1) and they accounted for a large

fraction of the variation in community composition attributed to environmental predictors (adjusted R^2 = 0.242; Table 1), which is nearly the same as the value for all 13 variables retained in the variation partitioning model (adjust R^2 = 0.264; Table 1).

(B) Conservation assessment

The species accumulation curves showed a levelling off at larger sample sizes for all vegetation types, although no curve actually reached an asymptote. Species accumulation curves levelled off less in vegetation types associated with rock outcrops (including *campos rupestres*) and in *Araucaria*-dominated forest (see Fig. S1). Because the overall floristic dissimilarity between cloud forests and rain forests was relatively low (Fig. 3), we assessed the rates of endemism considering these two vegetation types as 'core' habitats (wet forests in Table 2 and Fig. 5). Despite the fact that wet forests have twice as much protection as marginal habitats (45% and 26%, respectively; Table 2 and Figs. 5, 6 and 7), almost half of all species endemic to the Atlantic Domain are only found in marginal habitats (Table 2).

(A) DISCUSSION

Both the variation partitioning and the ordination support the importance of the set of limiting conditions proposed by Scarano (2009) as the factors controlling tree community composition of rain forests and marginal habitats, which are treated here in the context of 'marginal' vegetation types (*question i*). We also showed that these limiting factors lead to floristically distinct tree communities, thus indicating that the

444 marginal habitats are not simply a nested subset of the more diverse Atlantic Domain
445 rain forest (*question ii*). In fact, marginal habitats shelter nearly half the endemic tree
446 species in the Atlantic Domain (*question iii*).
447
448 **(B) Limiting factors**
449
450 A north to south increase in temperature seasonality is the major force
451 associated with a wide-scale floristic differentiation between tropical habitats and
452 those that are mainly comprised of cold-tolerant species (see Fig. 2a and Table 1).
453 Interestingly, this is consistent even within the subtropical section of the Atlantic
454 Domain (Oliveira-Filho *et al*., 2015), where variation in community composition along
455 the temperature seasonality gradient is congruent with an increasing foliage
456 deciduousness, a trait associated with frost-tolerance (Oliveira-Filho *et al*., 2015). A
457 similar trend in species turnover and foliage deciduousness also takes place in the
458 tropical and equatorial sections of the Atlantic Domain, but the main driving force
459 there is rainfall seasonality and the associated dry season (Eisenlohr & Oliveira-
460 Filho, 2015; Saiter *et al*., 2016). Contrary to our expectations, temperature
461 seasonality showed stronger explanatory power than the frequency of frosts,
462 believed to be a chief factor limiting species distribution across temperature
463 gradients (see Rundel *et al.*, 1994; Scarano, 2009; Zanne *et al.*, 2014; Oliveira-Filho
464 *et al*., 2015). Nevertheless, within rock outcrop habitats (Fig. 3b), the occurrence of
465 frost in rocky cloud dwarf-forests seems to be limiting the establishment of species
466 from *campos rupestres* and rocky semideciduous dwarf-forests, suggesting that the
467 frequency of frosts is an important factor underpinning the distribution of marginal
468 habitats in the Atlantic Domain, though at smaller spatial scales.

Periods of water shortage, i.e. seasonal droughts, are indeed the chief factor driving species turnover in the tropical and equatorial sections of the Atlantic Domain (see Fig. 2b), while other local factors may also affect water availability to plants (Pontara *et al*., 2016). The substrate often either favours or restricts water drainage via land-forms and soil depth and texture, whilst strong-winds may add to the water deficit stress, particular nearer to the coast, where *restingas* occur. In this coastal marginal habitat, which was identified as one of the most floristically differentiated (see Fig. 3a), the stress due to water deficit is certainly increased by a sandy substrate with high salinity, and by salt spray coming directly from the ocean (Cerqueira, 2000). In addition, although nutrient poor soils prevail all over the Domain, the edaphic conditions in *restingas* represent an extreme of particularly low soil fertility (most NTT sites of the dataset were classified as 'dystrophic' while most *restingas* were 'hypodystrophic').

When assessing whether soil waterlogging leads to a floristically distinct marginal habitat, we found that the intrusions of riverine forests into poorly drained soils of the Cerrado Domain showed only a weak differentiation from their neighbouring semideciduous forests (see Fig. 3). Kurtz *et al.* (2015) also found that riverine habitats of the Atlantic Domain are indistinguishable as a floristic unit from non-flooded habitats, and that their flora is essentially an extract of the regional species pool. These trends may result from a particular feature of the Atlantic Domain. Unlike the Amazon Domain, where a wide net of rivers lead to large areas of seasonally flooded habitats, rivers in the Atlantic Domain represent a minor component of the landscape. In the Amazon, seasonal flooding over wide alluvial beds is known as one of the main sources of floristic differentiation among habitat types and an important driver of tree species distribution patterns (Wittman *et al*.,

2013), whereas in the Atlantic Domain, the tiny areas of riverine forest are swamped with immigration from the non-flooded habitats. On the other hand, the intrusions of subtropical riverine forests into poorly drained soils of the Pampa Domain seems to have a comparatively stronger floristic differentiation (see Fig. 3a), but primarily associated with high temperature seasonality.

For *campos rupestres* we were able to document fire as an important factor limiting tree species distribution across the Atlantic Domain (see Fig. 3a). This is consistent with previous studies showing that forest-savanna boundaries in tropical savannas are driven by fire, though generally in interaction with other factors (Hoffman et al., 2013; Archibald et al., 2013; Dantas et al., 2013). Within the Atlantic Domain, however, fire frequency is low relative to the surrounding savanna formations (see detailed maps in Archibald et al., 2013) and has therefore been neglected in previous studies. Nevertheless, here we show that fire is actually an important component shaping macroscale patterns of floristic variation across the Atlantic Domain and, thus, deserves further attention. The congruence between floristic turnover and grass coverage, a proxy for fire frequency, across rocky semideciduous dwarf-forests and *campos rupestres* (Fig. 3a) indicates that fire plays a key role in determining the mosaic of rock outcrop habitats in the Atlantic Domain. Rocky semideciduous dwarf-forests seem to represent a transition between rain forests and *campos rupestres* (see Fig. 3a), which is likely to be mediated by fire history and local factors contributing to either increase or decrease flammability, particularly topography and soil depth.

(B) Spatial structure and unexplained variation

519 While the relevance of the environmental fraction in controlling community
520 turnover was straightforward to interpret, the variation that either remained
521 unexplained or was attributed to spatial structure independent of the measured
522 environmental factors (61% and 12%, respectively) deserves further attention. Rain
523 forests and marginal habitats are often geographically segregated (Fig. 2),
524 suggesting that there may be a role for spatially structured dispersal limitation and
525 historical biogeography in driving some of the observed floristic differentiation.
526 However, given the clear floristic segregation of rock outcrop dwarf-forests from
527 semideciduous and rain forests, despite their spatial interdigitation (e.g., in
528 southeastern Brazil; Fig. 2), we believe it is more parsimonious to attribute the
529 positive spatial autocorrelation, a proxy of distance decay in community similarity
530 (Nekola & White, 1999), to niche-based controls (e.g., unmeasured spatially
531 structured variables describing environmental conditions, natural enemies and
532 competition). Regarding the large fraction of unexplained variation, it may suggest
533 that ecological drift (cf. Hubbell, 2001) is driving stochastic rearrangements of
534 species distribution ranges through time. Although, a high proportion of unexplained
535 variation, ranging from 40% to 80% (e.g. Legendre et al., 2009; Neves et al., 2015;
536 reviewed by Soininen, 2014), is a common outcome in studies of floristic composition
537 over similar spatial scales, and could also be attributed to statistical noise (ter Braak,
538 1986; Guisan et al., 1999) or unmeasured non-spatially structured environmental
539 conditions.
540
541 **(B) Conservation implications**
542
543 Here we showed the uneven distribution of protected areas across the Atlantic

Domain with wet forests having twice as much protection. Marginal habitats receive considerably low protection, despite harbouring almost half of the 7,099 species endemic to the Atlantic Domain. These 3,160 endemic species are not found anywhere else in the world, including in the rain forests of the Atlantic Domain. This demonstrates that different marginal habitats, characterised by environmental harshness, underpin the patterns of high species richness across the Atlantic Domain as a whole. Therefore, we emphasize that these marginal habitats need better consideration by conservationists and biodiversity scientists, based on their (i) high level of endemism; (ii) lower level of protection; and (iii) less data (see species accumulation curves of vegetation types associated with rock outcrops in Fig. S1).

(B) Concluding remarks

The distribution of the Atlantic Forest marginal habitats is associated with low temperature extremes (i.e. ranging from winter frosts to summer maxima higher than 40ºC), soil salinity, drought-stress and soil waterlogging. Additionally, grass coverage, a proxy for flammability and a previously unappreciated environmental factor in the Atlantic Domain, is amongst the principal factors explaining the patterns of tree species distribution. For conservation purposes, the *restinga* is strikingly distinct both floristically and environmentally (see Figs. 3a-b), suggesting the need for further investigation. If *restingas* are indeed a distinct phytogeographical region, instead of an extension of rain forests into saline white-sand environments, they may be much more threatened than assumed based upon classifications that places these two habitats together. *Restinga* has suffered massive fragmentation due to high human occupation in coastal areas and a rapidly developing tourism industry.

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(A) REFERENCES

Ab'Sáber, A.N. (2003) *Os domínios de natureza no Brasil: potencialidades paisagísticas*. Ateliê Editorial, São Paulo.

Archibald, S., Lehmann, C.E.R., Goméz-Dans, J.L. & Bradstock, R.A. (2103) Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences U.S.A.*, **110**, 6442-6447.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Baselga, A. & Orme, D.I. (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, **3**, 808-812.

Blanchet, F.G, Legendre, P & Borcard, D. (2008) Forward selection of explanatory variables. *Ecology*, **89**, 2623-2632.

Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component

595 of ecological variation. *Ecology*, **73**, 1045-1055.
596 Borcard, D., Legendre, P., Avois-Jacquet, C. & Tuomisto, H. (2004) Dissecting the
597 spatial structure of ecological data at multiple scales. *Ecology*, **85**, 1826-1832.
598 ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector
599 technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.
600 Cerqueira, R. (2000) Biogeografia das restingas. *Ecologia de restingas e lagoas*
601 *costeiras* (ed. by F.A. Esteves and L.D. Lacerda), pp. 65-75. NUPEM/UFRJ,
602 Macaé, Brasil.
603 Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S-Y, Mao, C.X., Chazdon, R.L. & Longino,
604 J.T. (2012) Models and estimators linking individual-based and sample-based
605 rarefaction, extrapolation and comparison of assemblages. *Journal of Plant*
606 *Ecology*, **5**, 3–21.
607 Dantas, V.L., Batalha, M.A. & Pausas, J.G. (2013) Fire drives functional thresholds
608 on the savanna–forest transition. *Ecology*, **94**, 2454-2463.
609 Dray, S. (2010) *spacemakeR: spatial modelling*. R package version 473 0.0–5/r101.
610 Available at: http://R-Forge.R-project.org/projects/sedar/.
611 Eisenlohr, P.V. & Oliveira-Filho, A.T. (2015) Revisiting patterns of tree species
612 composition and their driving forces in the Atlantic forests of southeastern
613 Brazil. *Biotropica*, **47**, 689-701.
614 Galindo-Leal, C., Jacobsen, T.R., Langhammer, P.F. & Olivieri, S. (2003) State of
615 the hotspots: the dynamics of biodiversity loss. *The Atlantic Forest of South*
616 *America: biodiversity status, threats, and outlook* (ed. by C. Galindo-Leal C
617 and I.G. de Câmara), pp. 12–23. Center for Applied Biodiversity Science and
618 Island Press, Washington.
619 Guisan, A., Weiss, S.B. & Weiss, A.D. (1999) GLM versus CCA spatial modeling of

620 plant species distribution. *Plant Ecology*, **143**, 107–122.
621 Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L.,
622 Haridasan, M. & Franco, A.C. (2012) Ecological thresholds at the savanna-
623 forest boundary: how plant traits, resources and fire govern the distribution of
624 tropical biomes. *Ecology Letters*, **15**, 759-768.
625 Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*.
626 Princeton University Press, Princeton, NJ.
627 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high
628 resolution interpolated climate surfaces for global land areas. *International*
629 *Journal of Climatology*, **25**, 1965–1978.
630 IBGE (1993) *Mapa de Vegetação do Brasil*. Fundação Instituto Brasileiro de
631 Geografia e Estatística, Ministério da Agricultura, Rio de Janeiro.
632 Joly, C.A., Metzger, J.P. & Tabarelli, M. (2014) Experiences from the Brazilian
633 Atlantic forest: ecological findings and conservation initiatives. *New*
634 *Phytologist* **204**, 459–473.
635 Kent, M. & Coker, P. (1992) *Vegetation description and analysis: a practical*
636 *approach*. Belhaven, London.
637 Kurtz, B.C., Valentin, J.L. & Scarano, F.R. (2015) Are the Neotropical swamp forests
638 a distinguishable forest type? Patterns from Southeast and Southern Brazil.
639 *Edinburgh Journal of Botany*, **72**, 191-208.
640 Legendre, P. & Gallagher, E.D. (2001) Ecological meaningful transformations for
641 ordination of species data. *Oecologia*, **129**, 271-280.
642 Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M. & Myers, D. (2002)
643 The consequences of spatial structure for the design and analysis of
644 ecological field surveys. *Ecography*, **25**, 601-615.

645 Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I. & He, F. (2009) Partitioning
646 beta diversity in a subtropical broad-leaved forest of China. *Ecology*, **90**, 663-
647 674.
648 Legendre, P., Borcard, D. & Roberts, D.W. (2012) Variation partitioning involving
649 orthogonal spatial eigenfunction submodels. *Ecology*, **93**, 1234–1240.
650 Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S.,
651 Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J.M.,
652 Hutley, L.B., Ratnam, J., San Jose, J., Montes, R., Franklin, D., Russell-
653 Smith, J., Ryan, C.M., Durigan, G., Hiernaux, P., Haidar, R., Bowman, D.M.J.
654 S. & Bond, W.J. Savanna vegetation-fire-climate relationships differ among
655 continents. *Science*, **343**, 548-552.
656 Lepš, J. & Šmilauer, J.P. (2003) *Multivariate analysis of ecological data using*
657 *CANOCO*. Cambridge University Press, Cambridge, UK.
658 Lewin-Koh, N.J. & Bivand, R. (2012) *maptools: tools for reading and handling spatial*
659 *objects*. R package version 0.8–17/ r238. Available at: http://R-Forge.R
660 project.org/projects/maptools/.
661 McCune, B. & Grace, J.B. (2002) *Analysis of ecological communities*. MjM Software
662 Design, Gleneden Beach, Oregon.
663 Menini-Neto, L., Furtado, S.G., Zappi, D., Oliveira-Filho, A.T. & Forzza, R.C. (2016)
664 Biogeography of epiphytic Angiosperms in the Brazilian Atlantic forest, a world
665 biodiversity hotspot. *Brazilian Journal of Botany*, **39**, 261–273.
666 Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J. (2000)
667 Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
668 Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography
669 and ecology. *Journal of Biogeography*, **26**, 867-878.

670 Neves, D.M., Dexter, K.G., Pennington, R.T., Bueno, M.L. & Oliveira-Filho, A.T.
671 (2015) Environmental and historical controls of floristic composition across the
672 South American Dry Diagonal. *Journal of Biogeography*, **42**, 1566-1576.
673 Nychka, D., Furrer, R., Paige, J. & Sain, S. (2015) *fields: Tools for Spatial Data*. R
674 package version 8.3-5. Available at: http://CRAN.R-
675 project.org/package=fields.
676 Oliveira-Filho, A.T., Jarenkow, J.A. & Rodal, M.J.N. (2006) Floristic relationships of
677 seasonally dry forests of eastern South America based on tree species
678 distribution patterns. *Neotropical savannas and dry forests: plant diversity,*
679 *biogeography and conservation*. (ed. by R.T. Pennington, J.A. Ratter and G.P.
680 Lewis), pp. 151-184. CRC Press, Boca Raton, USA.
681 Oliveira-Filho, A.T., Fontes, M.A.L., Viana, P.L., Valente, A.S.M., Salimena, F.R.G. &
682 Ferreira, F.M. (2013) O mosaico de fitofisionomias do Parque Estadual do
683 Ibitipoca. Flora do Parque Estadual do Ibitipoca e seu entorno (ed. by R.C.
684 Forzza, L. Menini-Neto, F.R.G. Salimena and D. Zappi), pp. 53-93. Editora
685 UFJF, Juiz de Fora, Brazil.
686 Oliveira-Filho, A.T. (2015) Um Sistema de classificação fisionômico-ecológica da
687 vegetação Neotropical. *Fitossociologia no Brasil: Métodos e estudos de*
688 *casos, volume 2* (ed. by P.V. Eisenlohr, J.M. Felfili, M.M.R.F. Melo, L.A.
689 Andrade and J.A.A. Meira-Neto), pp. 452-473. Editora UFV, Viçosa, Brazil.
690 Oliveira-Filho, A.T., Budke, J.C., Jarenkow, J.A., Eisenlohr, P.V. & Neves, D.R.M.
691 (2015) Delving into the variations in tree species composition and richness
692 across South American subtropical Atlantic and Pampean forests. *Journal of*
693 *Plant Ecology*, **8**, 242-260.
694 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B.,

695 Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2016) *vegan:*
696 *community ecology package*. R package version 2.0–3. Available at:
697 http://CRAN.R-project.org/package=vegan.
698 Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning
699 of species data matrices: estimation and comparisons of fractions. *Ecology*,
700 **87**, 2614-2625.
701 Pontara, V., Bueno, M.L., Garcia, L.E., Oliveira-Filho, A.T., Pennington, R.T.
702 Burslem, D.F.R.P. & Lemos-Filho, J.P. (2016) Fine-scale variation in
703 topography and seasonality determine radial growth of an endangered tree in
704 Brazilian Atlantic forest. *Plant Soil*, **403**, 115-128.
705 Quinn, G.P. & Keough, M.J. (2002) *Experimental design and data analysis for*
706 *biologists*. Cambridge University Press, Cambridge, UK.
707 R Core Team (2015) *R: a language and environment for statistical computing*.
708 Version 3.1.0. R Foundation for Statistical Computing, Vienna. Available at:
709 http://www.Rproject.org/.
710 REFLORA, 2017. Lista de espécies da flora do Brasil. Jardim Botânico do Rio de
711 Janeiro, Brazil. http://floradobrasil.jbrj.gov.br/ (accessed 19.01.17).
712 Rundel, P.W., Smith, A.P. & Meinzer F. C. (1994) *Tropical alpine environments:*
713 *plant form and function*. Cambridge University Press, Cambridge, UK.
714 Saiter, F.Z., Eisenlohr, P.V., Barbosa, M.R., Thomas, W.W. & Oliveira-Filho, A.T.
715 (2016) From evergreen to deciduous tropical forests: how energy-water
716 balance, temperature, and space influence the tree species composition in a
717 high diversity region. *Plant Ecology & Diversity*, **9**, 45-54.
718 Santos, H.G., Jacomine, P.K.T., Anjos, L.H.C., Oliveira, V.A., Lumbreras, J.F.,
719 Coelho, M.R., Almeida, J.A., Cunha, T.J.F. & Oliveira, J.B. (2013) *Sistema*

720 *brasileiro de classificação de solos*, 3rd edn. Embrapa, Brasília.
721 Scarano, F.R. (2009) Plant communities at the periphery of the Atlantic rain forest:
722 Rare-species bias and its risks for conservation. *Biological Conservation*, **142**,
723 1201-1208.
724 Soininen, J. (2014) A quantitative analysis of species sorting across organisms and
725 ecosystems. *Ecology*, **95**, 3284–3292.
726 Tabarelli, M., Silva, J.M.C. & Gascon, C. (2004) Forest fragmentation, synergisms
727 and the impoverishment of neotropical forests. *Biodiversity and Conservation*,
728 **13**, 1419–1425.
729 Tabarelli, M., Pinto, L.P., Silva, J.M.C., Hirota, M. & Bedê, L. (2005) Challenges and
730 opportunities for biodiversity conservation in the Brazilian Atlantic Forest.
731 *Conservation Biology*, **19**, 695–700.
732 Tichý, L. & Chytrý, M. (2006) Statistical determination of diagnostic species for site
733 groups of unequal size. Journal of Vegetation Science, **17**, 809-818.
734 VanDerWal, J., Falconi, L., Januchowski, S., Shoo, L. & Storlie, C. (2014).
735 *SDMTools: Species Distribution Modelling Tools: tools for processing data*
736 *associated with species distribution modelling exercises*. R package version
737 1.1-221. Available at: https://CRAN.R-project.org/package=SDMTools
738 Walter, H. (1985) *Vegetation of the earth and ecological systems of the geo-*
739 *biosphere*, 3rd edn. Springer-Verlag, Berlin.
740 Wittmann, F., Householder, E., Piedade, M.T.F., Assis, R.L., Schöngart, J., Parolin,
741 P. & Junk, W.J. (2013) Habitat specificity, endemism and the neotropical
742 distribution of Amazonian white-water floodplain trees. *Ecography*, **36**, 690-
743 707.
744 Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G.,

McGlinn, D.J., Moles, A.T., O'Meara, B.C., Royer, D.L., Wright, I.J., Aarssen, L., Bertin, R.I., Govaerts, R., Hemmings, F., Leishman, M.R., Oleksyn, J., Reich, P.B., Sargent, R., Soltis, D.E., Soltis, P.S., Stevens, P.F., Swenson, N.G., Warman, L., Westoby, M. & Beaulieu, J.M. (2013) Three keys to the radiation of angiosperms into freezing environments. *Nature*, **506**, 89-92.

Zomer, R.J., Bossio, D.A., Trabucco, A., Yuanjie, L., Gupta, D.C. & Singh, V.P. (2007) *Trees and water: smallholder agroforestry on irrigated lands in northern India. IWMI Research Report 122*. International Water Management Institute, Colombo, Sri Lanka.

Zomer, R.J., Trabucco, A., Bossio, D.A., van Straaten, O. & Verchot, L.V. (2008) Climate change mitigation: a spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture Ecosystems and Environment*, **126**, 67-80.

(A) BIOSKETCH

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Author contributions: A.O.F compiled the database and conceived the idea; D.M.N. and K.G.D. designed the manuscript; D.M.N. analysed the data; D.M.N. and A.O.F. led the writing with substantial input from K.G.D, R.T.P. All authors commented on the manuscript and approved the final version.

Table 1 Variables selected for the study of environmental controls of tree community composition in the Atlantic Domain of South America. The variables shown were selected through a forward selection method for redundancy analysis and are ordered by the amount of explained variation in species composition across rain forest and marginal habitats. Goodness-of-fit of the predictor variables were assessed through adjusted coefficients of determination, Akaike Information Criterion (AIC), F-values and significance tests ($P < 0.01$ in all cases). VIF, variance inflation factor, obtained using the r-squared value of the regression of one variable against all other explanatory variables. adj. R^2 cum. = cumulative adjusted coefficient of correlation.

	adj. R^2 cum.	ΔAIC	F	VIF
Temperature seasonality	0.068	-508.02	128.96	3.51
Grass coverage	0.174	-716.16	34.28	1.28
Salinity	0.199	-767.24	27	2.04
Water deficit severity	0.209	-787.86	22.65	3.13
Hyperseasonality	0.222	-816.58	15.42	3.82
Mean annual precipitation	0.234	-840.26	13.41	2.57
Days of frost	0.242	-856.91	8.87	1.76
Elevation	0.251	-863.48	8.52	3.83
Temperature daily range	0.251	-875.73	7.8	2.64
Cloud interception	0.257	-887	4.89	3.27
Soil fertility	0.26	-892.36	4.6	1.46
Water excess duration	0.263	-896.43	3.73	3.11
Sandiness	0.264	-897.48	3	1.74

Table 2 Wet forests (rain forest + cloud forest) and marginal habitats of the South American Atlantic Domain ranked by their level of endemism in plant species (total endemics / total species richness). PA = percentage of NeoTropTree sites in protected areas (see Fig. S2, S3 and S4). Lists of plant species were obtained from the Reflora project (http://floradobrasil.jbrj.gov.br).

	All				Endemics					
	Angiosperms	Pteridophyta	Gymnosperms	Total	Angiosperms	Pteridophyta	Gymnosperms	Total endemics	%	PA (%)
wet forests	8,938	755	2	9,695	3,740	199	-	3,939	41	45
campos rupestres	4,936	57	-	4,993	1,953	15	-	1968	39	54
rocky cloud dwarf-forest	2,037	97	2	2,136	429	19	-	448	21	73
restinga	2,490	38	2	2,530	297	1	-	298	12	51
semideciduous forest	3,362	165	1	3,528	243	4	-	247	7	19
rocky semideciduous dwarf-forest	878	21	1	900	8	-	-	8	1	52
Araucaria-dominated forest	1,348	155	4	1,507	81	6	-	87	6	17
tropical riverine forest	2,495	61	5	2,561	101	2	1	104	4	21
subtropical riverine forest	231	2	1	234	-	-	-	-	-	1

Figure Captions

Figure 1 Environmental variables (arrows) hypothesized in Scarano (2009) as key factors limiting plant species distribution across the Atlantic Domain of South America. The harshest extremes give rise to distinct vegetation types, referred to as marginal habitats. Coastal white-sand woodlands are called *restinga* in Brazil.

Figure 2 Distribution of 1,753 Atlantic Domain sites with their *a priori* classification into vegetation types (symbols). Variation in (a) temperature seasonality (standard deviation x100) and (b) water deficit severity (mm) was fitted across geographic space by generalized additive model. Dashed lines represent Brazilian state borders.

Figure 3 Ordination of 1,753 Atlantic Domain sites yielded by non-metric multidimensional scaling (NMDS) of their tree species composition with their *a priori* classification into vegetation types (symbols). Diagrams are provided for axes 1 x 2 (a) and 1 x 3 (b). Arrows in each diagram represent the correlations between the most explanatory environmental variables and ordination scores. TempSeas = temperature seasonality; DaysFrost = days of frost; salinity = soil salinity; GrassCover = grass coverage; HyperSeas = water hyperseasonality; PrecAnn = mean annual precipitation.

Figure 4 Decomposition of the pairwise floristic dissimilarity of rain forest and marginal habitat sites of the South American Atlantic Domain (e.g. bullets in the *Araucaria*-dominated triangle represent pairwise dissimilarities between each of the

193 *Araucaria*-dominated sites and all the 328 rain forest sites; i.e. 63,304 pairwise dissimilarity values). Numbers represent the mean turnover (%) and nestedness (%) components of the Jaccard dissimilarity for each marginal habitat.

Figure 5 Conservation assessment of wet forests (rain + cloud), rocky cloud dwarf-forest and *Araucaria*-dominated forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders.

Figure 6 Conservation assessment of *campo rupestre*, semideciduous forests and rocky semideciduous dwarf-forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders.

Figure 7 Conservation assessment of *restinga*, subtropical riverine forests and tropical riverine forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders. Coastal white-sand woodlands are called *restinga* in Brazil.

DATA ACCESSIBILITY

Additional accessibility data is provided as supporting information.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Figure S1 Species accumulation curve per vegetation type, using a sample-based rarefaction method. Grey shadow shows confidence intervals from standard deviation.

Table S1 Relationship between habitat quality and variation in tree community composition across the Atlantic Domain of South America. The variables shown were selected through a forward selection method for redundancy analysis and are ordered by the amount of explained variation in species composition variation across rain forests and marginal habitats. Goodness-of-fit of the predictor variables were assessed through adjusted coefficients of determination, Akaike Information Criterion (AIC), F-values and significance tests ($P < 0.01$ in all cases). adj. R^2 cum. = cumulative adjusted coefficient of correlation.

Table S2 Top 50 diagnostic species of the five marginal and stressing habitats of the Atlantic Domain defined by the main explanatory environmental emerging from the community turnover models. The top 50 diagnostic species of the non-stressed habitat (i.e. wet habitat) of the Atlantic Domain are also given.

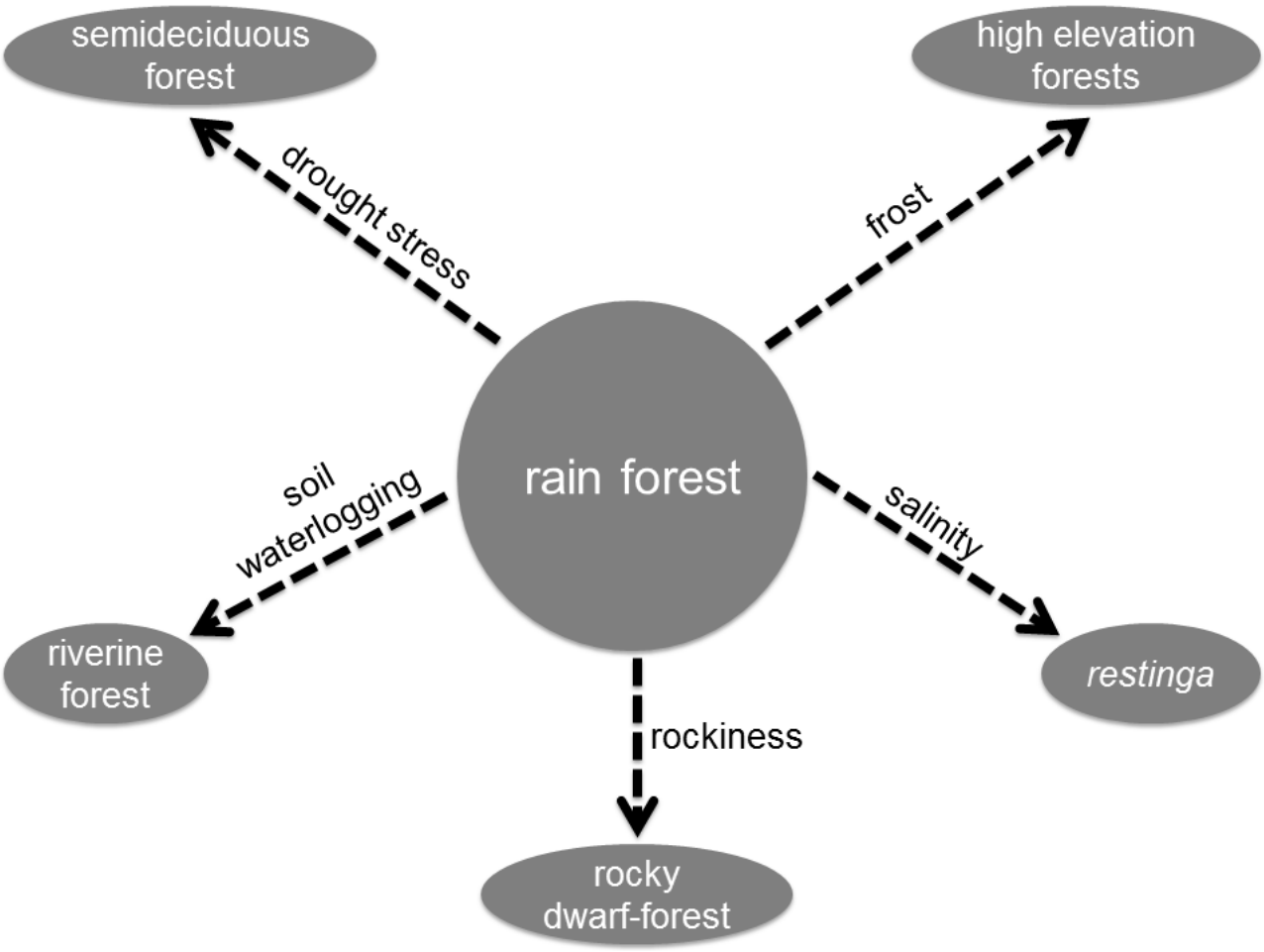

Figure 1 Environmental variables (arrows) hypothesized in Scarano (2009) as key factors limiting plant species distribution across the Atlantic Domain of South America. The harshest extremes give rise to distinct vegetation types, referred to as marginal habitats. Coastal white-sand woodlands are called *restinga* in Brazil.

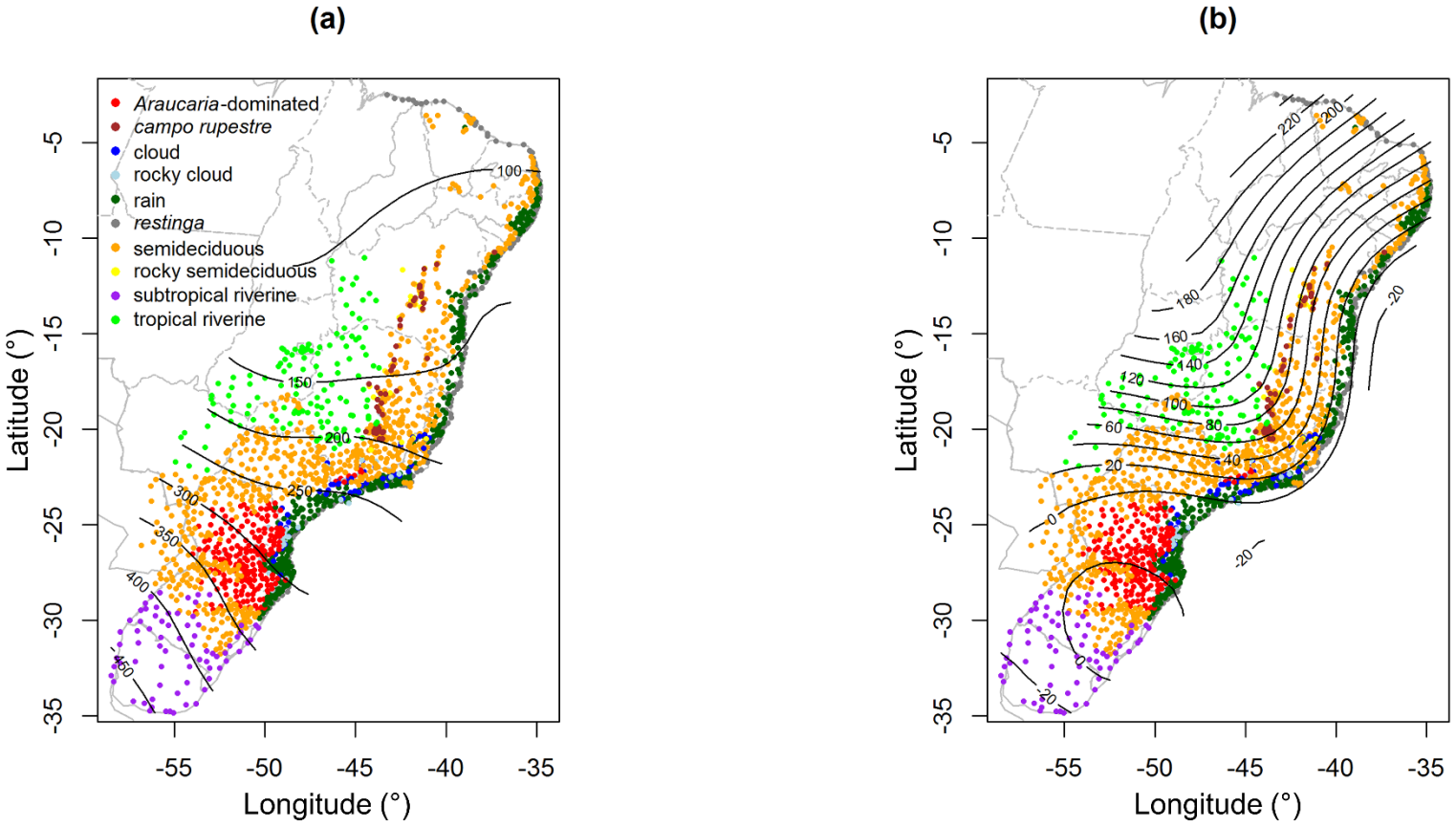

Figure 2 Distribution of 1,753 Atlantic Domain sites with their *a priori* classification into vegetation types (symbols). Variation in (a) temperature seasonality (standard deviation *100) and (b) water deficit severity (mm) was fitted across geographic space by generalized additive model. Dashed lines represent Brazilian state borders.

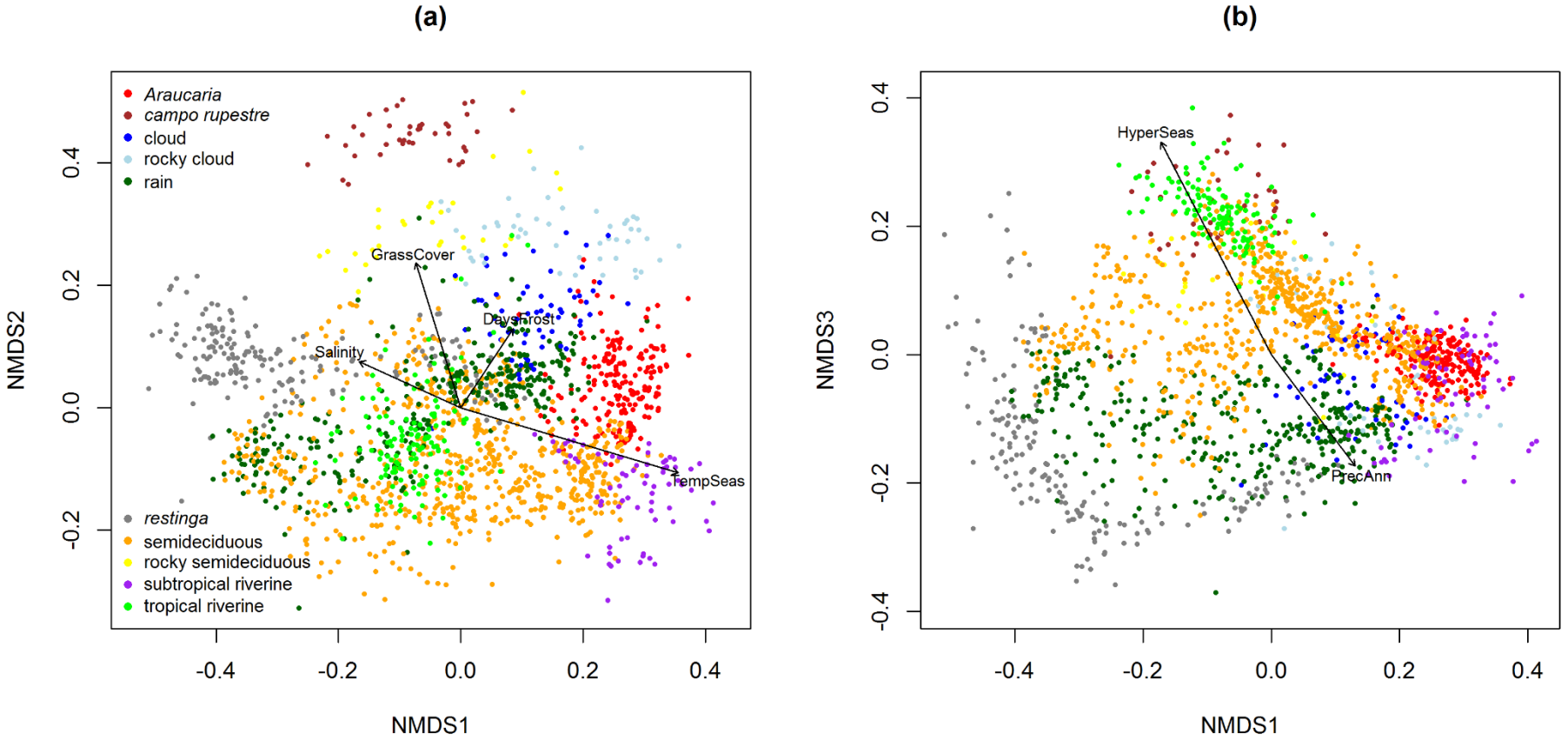

Figure 3 Ordination of 1,753 Atlantic Domain sites yielded by non-metric multidimensional scaling (NMDS) of their tree species composition with their a priori classification into vegetation types (symbols). Diagrams are provided for axes 1 x 2 (a) and 1 x 3 (b). Arrows in each diagram represent the correlations between the most explanatory environmental variables and ordination scores. TempSeas = temperature seasonality; DaysFrost = days of frost; salinity = soil salinity; GrassCover = grass coverage; HyperSeas = water hyperseasonality; PrecAnn = mean annual precipitation.

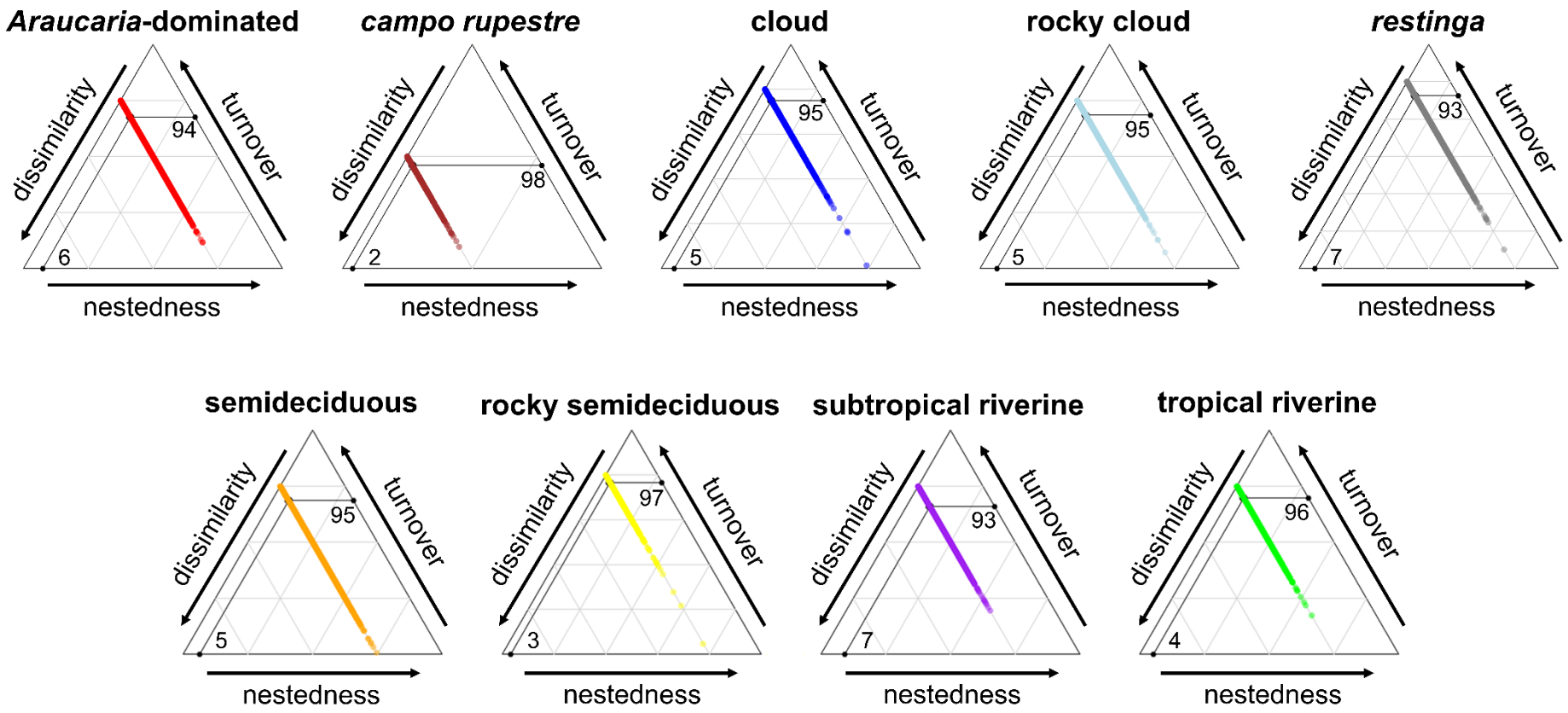

Figure 4 Decomposition of the pairwise floristic dissimilarity between marginal and rain forest sites of the South American Atlantic Domain (e.g. bullets in the *Araucaria*-dominated triangle represent pairwise dissimilarities between each of the 193 *Araucaria*-dominated forest sites and all the 328 rain forest sites; i.e. 63,304 pairwise dissimilarity values). Numbers represent the mean turnover (%) and nestedness (%) components of the Jaccard dissimilarity for each marginal habitat.

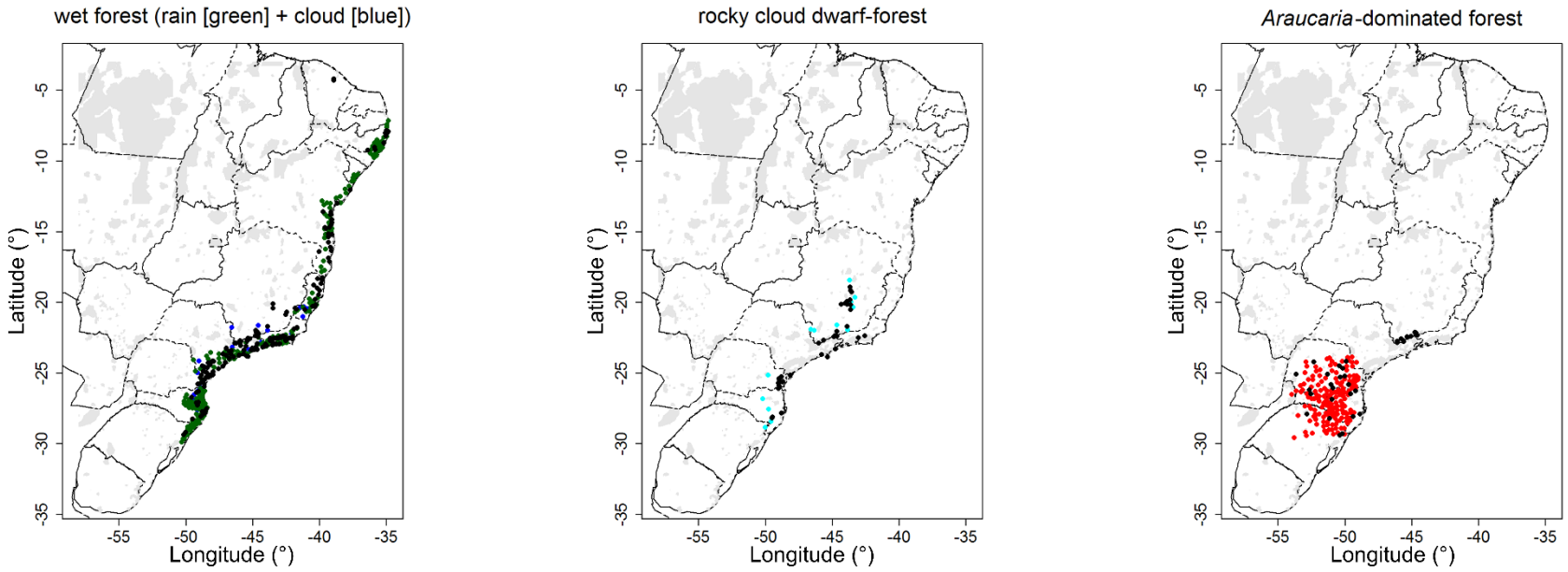

Figure 5 Conservation assessment of wet forests (rain + cloud), rocky cloud dwarf-forests and *Araucaria*-dominated forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders.

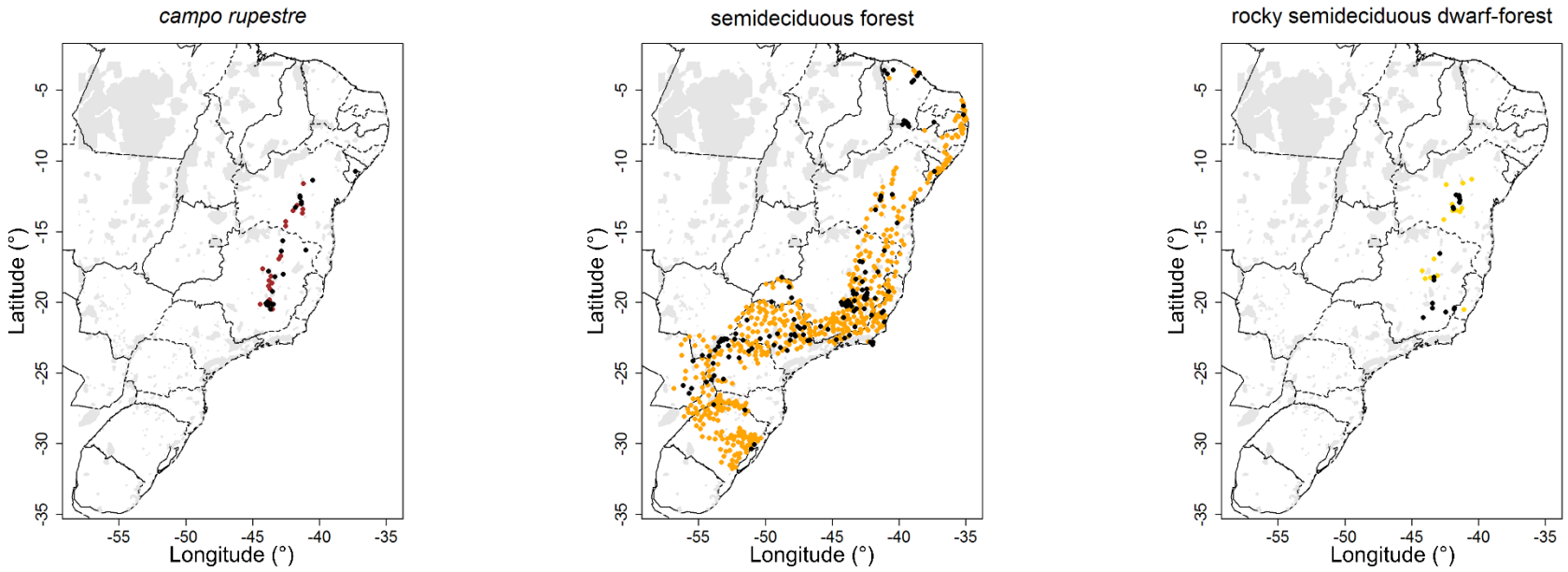

Figure 6 Conservation assessment of *campo rupestre*, semideciduous forests and rocky semideciduous dwarf-forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders.

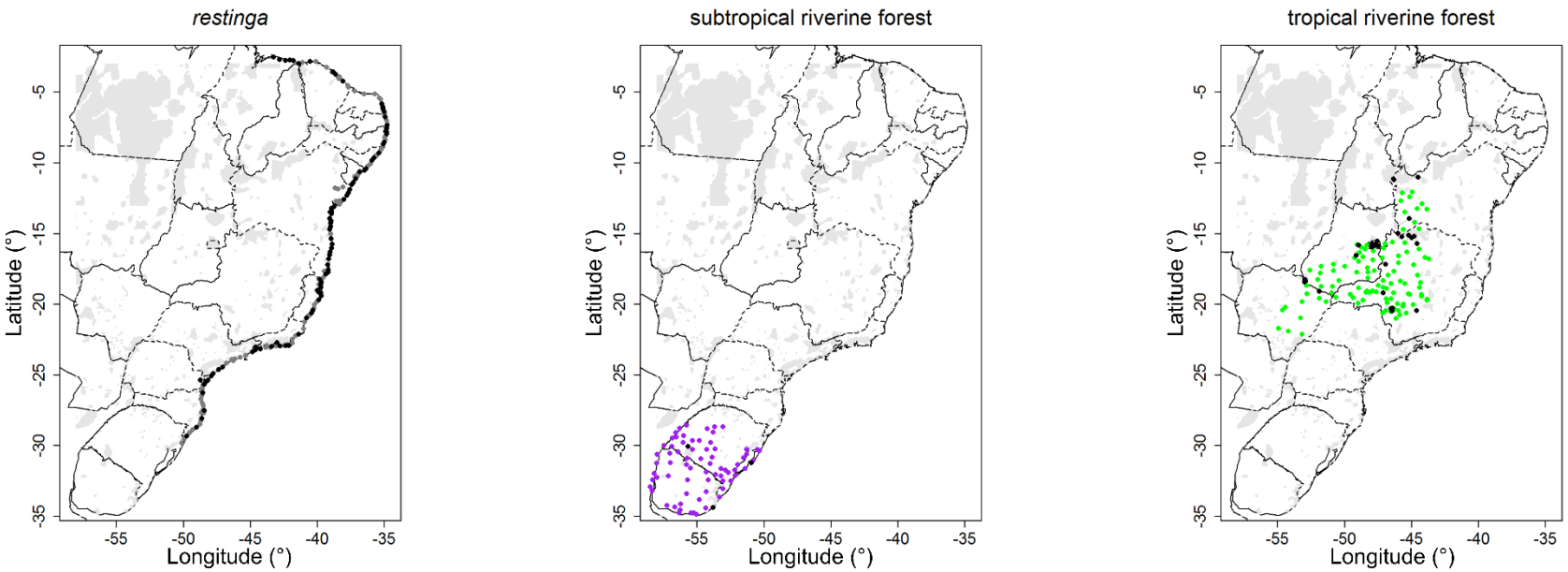

Figure 7 Conservation assessment of *restinga*, subtropical riverine forests and tropical riverine forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders.

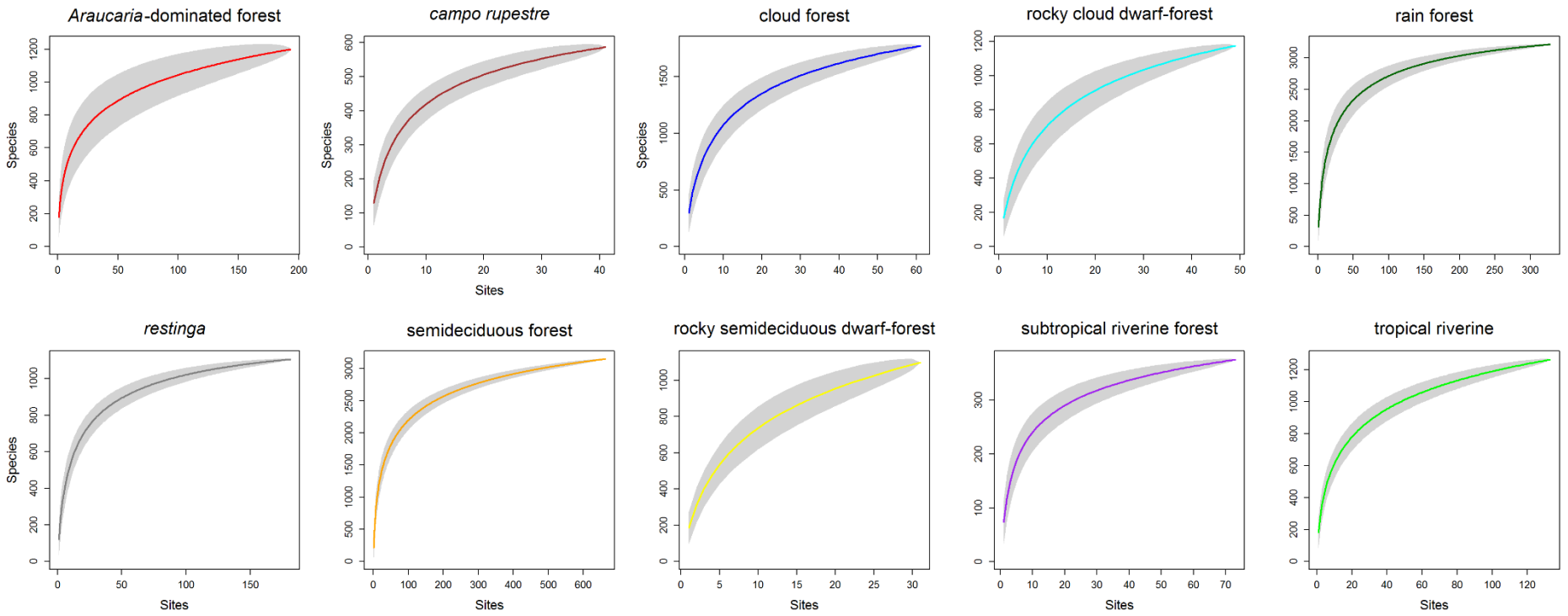

Figure S1 Species accumulation curve per vegetation type, using a sample-based rarefaction method. Grey shadow shows confidence intervals from standard deviation.

Table S1 Relationship between habitat quality and variation in tree community composition across the Atlantic Domain of South America. The variables shown were selected through a forward selection method for redundancy analysis and are ordered by the amount of explained variation in species composition across rain forests and marginal habitats. Goodness-of-fit of the predictor variables were assessed through adjusted coefficients of determination, Akaike Information Criterion (AIC), F-values and significance tests (P < 0.01 in all cases). adj. R^2 cum. = cumulative adjusted coefficient of correlation.

	adj. R^2	ΔAIC	F
Patch area	0.003	-316.83	5.183
Edge perimeter	0.005	-317.83	3.003
Core area index	0.005	-317.86	2.019
Fractal dimension index	0.006	-317.78	1.917

Table S2 Top 50 diagnostic species of the five marginal and stressing habitats of the Atlantic Domain defined by the main explanatory environmental emerging from the community turnover models. The top 50 diagnostic species of the non-stressed habitat (i.e. rain forests) of the Atlantic Forest Domain are also given.

Stressed marginal habitat: seasonally dry	
Families	Species
Anacardiaceae	*Astronium fraxinifolium* Schott
Anacardiaceae	*Myracrodruon urundeuva* Allemão
Apocynaceae	*Aspidosperma cuspa* (Kunth) S.F.Blake ex Pittier
Apocynaceae	*Aspidosperma cylindrocarpon* Müll.Arg.
Apocynaceae	*Aspidosperma subincanum* Mart. ex A.DC.
Arecaceae	*Acrocomia aculeata* (Jacq.) Lodd. ex Mart.
Bignoniaceae	*Handroanthus impetiginosus* Mattos
Bignoniaceae	*Jacaranda cuspidifolia* Mart. ex A.DC.
Bignoniaceae	*Tabebuia roseoalba* (Ridl.) Sandwith
Bignoniaceae	*Zeyheria tuberculosa* (Vell.) Bureau
Combretaceae	*Terminalia argentea* Mart.
Combretaceae	*Terminalia fagifolia* Mart.
Ebenaceae	*Diospyros hispida* A.DC.
Euphorbiaceae	*Manihot carthagenensis* (Jacq.) Müll.Arg.
Icacinaceae	*Emmotum nitens* (Benth.) Miers
Leguminosae	*Albizia niopoides* (Spruce ex Benth.) Burkart
Leguminosae	*Anadenanthera peregrina* (L.) Speg.
Leguminosae	*Apuleia leiocarpa* (Vogel) J.F.Macbr.
Leguminosae	*Bowdichia virgilioides* Kunth
Leguminosae	*Chloroleucon acacioides* (Ducke) Barneby & J.W.Grimes
Leguminosae	*Dipteryx alata* Vogel
Leguminosae	*Enterolobium contortisiliquum* (Vell.) Morong
Leguminosae	*Hymenaea martiana* Hayne
Leguminosae	*Machaerium acutifolium* Vogel
Leguminosae	*Machaerium hirtum* (Vell.) Stellfeld
Leguminosae	*Pityrocarpa* moniliformis (Benth.) Luckow & R.W.Jobson
Leguminosae	*Plathymenia reticulata* Benth.
Leguminosae	*Platypodium elegans* Vogel
Leguminosae	*Pterodon* emarginatus Vogel
Leguminosae	*Pterogyne nitens* Tul.
Leguminosae	*Senna velutina* (Vogel) H.S.Irwin & Barneby
Leguminosae	*Sweetia fruticosa* Spreng.
Malpighiaceae	*Heteropterys byrsonimifolia* A.Juss.
Malvaceae	*Guazuma ulmifolia* Lam.
Malvaceae	*Luehea grandiflora* Mart. & Zucc.

Malvaceae	*Sterculia striata* A.St.-Hill. & Naudin
Moraceae	*Maclura tinctoria* (L.) D.Don ex Steud.
Myrtaceae	*Campomanesia velutina* (Cambess.) O.Berg
Myrtaceae	*Eugenia stictopetala* DC.
Myrtaceae	*Myrcia tomentosa* (Aubl.) DC.
Myrtaceae	*Psidium guineense* Sw.
Nyctaginaceae	*Guapira graciliflora* (Mart. ex J.A.Schmidt) Lundell
Opiliaceae	*Agonandra brasiliensis* Miers ex Benth. & Hook.f.
Phyllanthaceae	*Phyllanthus acuminatus* Vahl
Proteaceae	*Euplassa inaequalis* (Pohl) Engl.
Rhamnaceae	*Rhamnidium elaeocarpum* Reissek
Rubiaceae	*Simira corumbensis* (Standl.) Steyerm.
Rutaceae	*Zanthoxylum riedelianum* Engl.
Salicaceae	*Casearia gossypiosperma* Briq.
Sapindaceae	*Talisia esculenta* (A.St.-Hil.) Radlk.
Verbenaceae	*Aloysia virgata* (Ruiz & Pav.) Juss.

Stressed marginal habitat: low temperature extremes

Families	Species
Anacardiaceae	*Lithrea brasiliensis* Marchand
Anacardiaceae	*Schinus engleri* F.A.Barkley
Annonaceae	*Annona rugulosa* (Schltdl.) H.Rainer
Aquifoliaceae	*Ilex brevicuspis* Reissek
Aquifoliaceae	*Ilex microdonta* Reissek
Aquifoliaceae	*Ilex paraguariensis* A.St.-Hil.
Araucariaceae	*Araucaria angustifolia* (Bertol.) Kuntze
Asparagaceae	*Cordyline spectabilis* Kunth & Bouché
Asteraceae	*Baccharis semiserrata* DC.
Asteraceae	*Piptocarpha angustifolia* Dusén ex Malme
Asteraceae	*Vernonanthura discolor* (Spreng.) H.Rob.
Bignoniaceae	*Handroanthus albus* (Cham.) Mattos
Canellaceae	*Cinnamodendron dinisii* Schwacke
Celastraceae	*Maytenus ilicifolia* Mart. ex Reissek
Cyatheaceae	*Alsophila setosa* Kaulf.
Dicksoniaceae	*Dicksonia* sellowiana Hook.
Euphorbiaceae	*Gymnanthes* klotzschiana Müll.Arg.
Euphorbiaceae	*Manihot* grahamii Hook.
Euphorbiaceae	*Sebastiania brasiliensis* Spreng.
Lamiaceae	*Vitex megapotamica* (Spreng.) Moldenke
Lauraceae	*Cinnamomum amoenum* (Nees & Mart.) Kosterm.
Lauraceae	*Nectandra lanceolata* Nees
Lauraceae	*Nectandra megapotamica* (Spreng.) Mez
Lauraceae	*Ocotea porosa* (Nees & Mart.) Barroso
Lauraceae	*Ocotea puberula* (Rich.) Nees
Lauraceae	*Ocotea pulchella* (Nees & Mart.) Mez
Leguminosae	*Mimosa scabrella* Benth.
Melastomataceae	*Leandra regnellii* (Triana) Cogn.

Melastomataceae	*Miconia cinerascens* Miq.
Monimiaceae	*Hennecartia omphalandra* J.Poiss.
Myrtaceae	*Acca sellowiana* (O.Berg) Burret
Myrtaceae	*Calyptranthes concinna* DC.
Myrtaceae	*Campomanesia xanthocarpa* (Mart.) O.Berg
Myrtaceae	*Eugenia uruguayensis* Cambess.
Myrtaceae	*Myrceugenia euosma* (O.Berg) D.Legrand
Myrtaceae	*Myrceugenia glaucescens* (Cambess.) D.Legrand & Kausel
Myrtaceae	*Myrcianthes gigantea* (D.Legrand) D.Legrand
Myrtaceae	*Myrrhinium atropurpureum* Schott
Rutaceae	*Zanthoxylum fagara* (L.) Sarg.
Salicaceae	*Banara tomentosa* Clos
Salicaceae	*Xylosma tweediana* (Clos) Eichler
Sapindaceae	*Allophylus guaraniticus* (A.St.-Hil.) Radlk.
Sapindaceae	*Cupania vernalis* Cambess.
Sapindaceae	*Matayba elaeagnoides* Radlk.
Solanaceae	*Solanum mauritianum* Scop.
Solanaceae	*Solanum pseudo*-quina A.St.-Hil.
Solanaceae	*Solanum sanctae*-catharinae Dunal
Solanaceae	*Solanum variabile* Mart.
Styracaceae	*Styrax leprosus* Hook. & Arn.
Symplocaceae	*Symplocos uniflora* (Pohl) Benth.

Stressed marginal habitat: high salinity	
Families	Species
Anacardiaceae	*Anacardium occidentale* L.
Annonaceae	*Annona acutiflora* Mart.
Apocynaceae	*Aspidosperma pyricollum* Müll.Arg.
Aquifoliaceae	*Ilex integerrima* (Vell.) Reissek
Aquifoliaceae	*Ilex psammophila* Reissek
Arecaceae	*Syagrus schizophylla* (Mart.) Glassman
Bignoniaceae	*Jacaranda bracteata* Bureau & K.Schum
Boraginaceae	*Cordia restingae* M.Stapf
Cactaceae	*Cereus fernambucensis* Lem.
Calophyllaceae	*Kielmeyera neglecta* Saddi
Celastraceae	*Maytenus distichophylla* Mart. ex Reissek
Celastraceae	*Maytenus littoralis* Car.-Okano
Chrysobalanaceae	*Chrysobalanus icaco* L.
Chrysobalanaceae	*Couepia schottii* Fritsch
Clusiaceae	*Clusia fluminensis* Planch. & Triana
Combretaceae	*Combretum glaucocarpum* Mart.
Ebenaceae	*Diospyros gaultheriifolia* Mart.
Euphorbiaceae	*Croton sphaerogynus* Baill.
Humiriaceae	*Humiriastrum spiritu-sancti* Cuatrec.
Lauraceae	*Ocotea arenicola* L.C.S.Assis & Mello-Silva
Leguminosae	*Abarema filamentosa* (Benth.) Pittier
Leguminosae	*Brodriguesia santosii* R.S.Cowan

Leguminosae	*Copaifera arenicola* (Ducke) J.Costa & L.P.Queiroz
Leguminosae	*Inga maritima* Benth.
Leguminosae	*Macrolobium rigidum* R.S.Cowan
Leguminosae	*Moldenhawera blanchetiana* Tul.
Melastomataceae	*Miconia francavillana* Cogn.
Melastomataceae	*Mouriri cearensis* Huber
Melastomataceae	*Tibouchina francavillana* Cogn.
Myrtaceae	*Calycolpus legrandii* Mattos
Myrtaceae	*Calyptranthes restingae* Sobral
Myrtaceae	*Eugenia azeda* Sobral
Myrtaceae	*Eugenia ilhensis* O.Berg
Myrtaceae	*Myrcia hirtiflora* DC.
Myrtaceae	*Myrcia insularis* Gardner
Myrtaceae	*Myrcia littoralis* DC.
Myrtaceae	*Myrcia lundiana* Kiaersk.
Myrtaceae	*Myrcia ovata* Cambess.
Myrtaceae	*Myrcia rotundifolia* (O.Berg) Kiaersk.
Nyctaginaceae	*Guapira pernambucensis* (Casar.) Lundell
Olacaceae	*Dulacia papillosa* (Rangel) Sleumer
Primulaceae	*Jacquinia armillaris* Jacq.
Primulaceae	*Myrsine parvifolia* DC.
Rhamnaceae	*Scutia arenicola* (Casar.) Reissek
Rubiaceae	*Melanopsidium nigrum* Colla
Rubiaceae	*Tocoyena bullata* (Vell.) Mart.
Sapindaceae	*Matayba livescens* (Radlk.) R.L.G.Coelho, Souza & Ferrucci
Sapotaceae	*Manilkara triflora* (Allemão) Monach.
Ximeniaceae	*Ximenia americana* L.

Stressed marginal habitat: high grass coverage

Families	Species
Araliaceae	*Schefflera macrocarpa* (Cham. & Schltdl.) Frodin
Asteraceae	*Baccharis retusa* DC.
Asteraceae	*Eremanthus capitatus* (Spreng.) MacLeish
Asteraceae	*Eremanthus glomerulatus* Less.
Asteraceae	*Eremanthus incanus* (Less.) Less.
Asteraceae	*Eremanthus polycephalus* (DC.) MacLeish
Asteraceae	*Lychnophora ericoides* Mart.
Asteraceae	*Lychnophora pinaster* Mart.
Asteraceae	*Lychnophora salicifolia* Mart.
Asteraceae	*Moquinia racemosa* (Spreng.) DC.
Asteraceae	*Moquiniastrum paniculatum* (Less.) G.Sancho
Asteraceae	*Paralychnophora bicolor* (DC.) MacLeish
Asteraceae	*Wunderlichia mirabilis* Riedel ex Baker
Bignoniaceae	*Handroanthus ochraceus* (Cham.) Mattos
Calophyllaceae	*Kielmeyera petiolaris* Mart.
Celastraceae	*Plenckia populnea* Reissek
Clusiaceae	*Clusia nemorosa* G.Mey.

Ericaceae	*Agarista coriifolia* (Thunb.) Hook.f. ex Nied.
Ericaceae	*Agarista glaberrima* (Sleumer) Judd
Ericaceae	*Gaylussacia brasiliensis* (Spreng.) Meisn.
Ericaceae	*Gaylussacia montana* (Pohl) Sleumer
Euphorbiaceae	*Stillingia saxatilis* Müll.Arg.
Lamiaceae	*Aegiphila verticillata* Vell.
Lauraceae	*Ocotea percoriacea* Kosterm.
Lauraceae	*Ocotea pomaderroides* (Meisn.) Mez
Leguminosae	*Calliandra asplenioides* (Nees) Renvoize
Leguminosae	*Chamaecrista brachystachya* (Benth.) Conc., L.P.Queiroz & G.P.Lewis
Leguminosae	*Chamaecrista cytisoides* (DC. ex Collad.) H.S.Irwin & Barneby
Leguminosae	*Dalbergia miscolobium* Benth.
Leguminosae	*Stryphnodendron adstringens* (Mart.) Coville
Malpighiaceae	*Byrsonima variabilis* A.Juss.
Melastomataceae	*Miconia albicans* (Sw.) Triana
Melastomataceae	*Miconia theizans* (Bonpl.) Cogn.
Melastomataceae	*Trembleya parviflora* (D.Don) Cogn.
Myrtaceae	*Calyptranthes brasiliensis* Spreng.
Myrtaceae	*Eugenia punicifolia* (Kunth) DC.
Myrtaceae	*Eugenia vetula* DC.
Myrtaceae	*Myrcia mischophylla* Kiaersk.
Myrtaceae	*Myrcia mutabilis* (O.Berg) N.Silveira
Primulaceae	*Myrsine emarginella* Miq.
Primulaceae	*Myrsine guianensis* (Aubl.) Kuntze
Rubiaceae	*Cordiera elliptica* (Cham.) Kuntze
Rubiaceae	*Cordiera vinosa* (Cham.) Kuntze
Salicaceae	*Casearia eichleriana* Sleumer
Styracaceae	*Styrax aureus* Mart.
Symplocaceae	*Symplocos oblongifolia* Casar.
Vochysiaceae	*Qualea cordata* (Mart.) Spreng.
Vochysiaceae	*Vochysia elliptica* Mart.
Vochysiaceae	*Vochysia emarginata* (Vahl) Poir.
Vochysiaceae	*Vochysia thyrsoidea* Pohl

Stressed marginal habitat: waterlogged riverine	
Families	Species
Annonaceae	*Cardiopetalum calophyllum* Schltdl.
Annonaceae	*Guatteria sellowiana* Schltdl.
Annonaceae	*Unonopsis guatterioides* (A.DC.) R.E.Fr.
Annonaceae	*Xylopia emarginata* Mart.
Aquifoliaceae	*Ilex integerrima* (Vell.) Reissek
Arecaceae	*Butia yatay* (Mart.) Becc.
Arecaceae	*Mauritia flexuosa* L.f.
Bignoniaceae	*Jacaranda brasiliana* (Lam.) Pers.
Burseraceae	*Protium spruceanum* (Benth.) Engl.
Calophyllaceae	*Calophyllum brasiliense* Cambess.
Cannabaceae	*Celtis chichape* (Wedd.) Miq.

Celastraceae	*Cheiloclinium cognatum* (Miers) A.C.Sm.
Celastraceae	*Maytenus floribunda* Reissek
Chrysobalanaceae	*Hirtella* glandulosa Spreng.
Chrysobalanaceae	*Licania* apetala (E.Mey.) Fritsch
Erythropalaceae	*Heisteria ovata* Benth.
Euphorbiaceae	*Gymnanthes schottiana* Müll.Arg.
Euphorbiaceae	*Maprounea guianensis* Aubl.
Lauraceae	*Aniba heringeri* Vattimo-Gil
Lauraceae	*Nectandra cissiflora* Nees
Lauraceae	*Nectandra warmingii* Meisn.
Lauraceae	*Ocotea spixiana* (Nees) Mez
Leguminosae	*Albizia inundata* (Mart.) Barneby & J.W.Grimes
Leguminosae	*Hymenolobium heringeranum* Rizzini
Leguminosae	*Inga alba* (Sw.) Willd.
Leguminosae	*Inga laurina* (Sw.) Willd.
Leguminosae	*Inga nobilis* Willd.
Leguminosae	*Tachigali rubiginosa* (Mart. ex Tul.) Oliveira-Filho
Melastomataceae	*Miconia cuspidata* Mart. ex Naudin
Melastomataceae	*Miconia* elegans Cogn.
Melastomataceae	*Tococa* guianensis Aubl.
Moraceae	*Ficus obtusifolia* Kunth
Moraceae	*Ficus obtusiuscula* (Miq.) Miq.
Moraceae	*Pseudolmedia laevigata* Trécul
Myristicaceae	*Virola sebifera* Aubl.
Myrtaceae	*Eugenia uruguayensis* Cambess.
Myrtaceae	*Myrcia fenzliana* O.Berg
Myrtaceae	*Myrcianthes cisplatensis* (Cambess.) O.Berg
Oleaceae	*Chionanthus trichotomus* (Vell.) P.S.Green
Phyllanthaceae	*Richeria grandis* Vahl
Picramniaceae	*Picramnia sellowii* Planch.
Primulaceae	*Myrsine leuconeura* Mart.
Primulaceae	*Myrsine parvifolia* DC.
Rubiaceae	*Faramea latifolia* (Cham. & Schltdl.) DC.
Rubiaceae	*Ferdinandusa speciosa* Pohl
Rubiaceae	*Ixora brevifolia* Benth.
Salicaceae	*Salix humboldtiana* Willd.
Sapotaceae	*Micropholis venulosa* (Mart. & Eichler) Pierre
Verbenaceae	*Citharexylum montevidense* (Spreng.) Moldenke
Vochysiaceae	*Callisthene major* Mart.

Atlantic Forest non-marginal habitats: stressed essentially by light

Families	Species
Annonaceae	*Annona neosericea* H.Rainer
Aquifoliaceae	*Ilex paraguariensis* A.St.-Hil.
Aquifoliaceae	*Ilex theezans* Mart. ex Reissek
Arecaceae	*Geonoma schottiana* Mart.
Asteraceae	*Vernonanthura discolor* (Spreng.) H.Rob.

Asteraceae	*Vernonanthura puberula* (Less.) H.Rob.
Bignoniaceae	*Jacaranda micrantha* Cham.
Bignoniaceae	*Jacaranda puberula* Cham.
Cyatheaceae	*Alsophila setosa* Kaulf.
Dicksoniaceae	*Dicksonia sellowiana* Hook.
Euphorbiaceae	*Alchornea sidifolia* Müll.Arg.
Lamiaceae	*Vitex megapotamica* (Spreng.) Moldenke
Lauraceae	*Aniba firmula* (Nees & Mart.) Mez
Lauraceae	*Cryptocarya aschersoniana* Mez
Lauraceae	*Nectandra grandiflora* Nees
Lauraceae	*Nectandra megapotamica* (Spreng.) Mez
Lauraceae	*Nectandra membranacea* (Sw.) Griseb.
Lauraceae	*Nectandra oppositifolia* Nees
Lauraceae	*Nectandra puberula* (Schott) Nees
Lauraceae	*Ocotea bicolor* Vattimo-Gil
Lauraceae	*Ocotea odorifera* (Vell.) Rohwer
Lauraceae	*Ocotea porosa* (Nees & Mart.) Barroso
Lauraceae	*Ocotea puberula* (Rich.) Nees
Lauraceae	*Persea willdenovii* Kosterm.
Leguminosae	*Inga sessilis* (Vell.) Mart.
Leguminosae	*Tachigali denudata* (Vogel) Oliveira-Filho
Malpighiaceae	*Byrsonima ligustrifolia* A.Juss.
Melastomataceae	*Miconia cabucu* Hoehne
Melastomataceae	*Miconia cinerascens* Miq.
Melastomataceae	*Miconia pusilliflora* (DC.) Naudin
Melastomataceae	*Tibouchina pulchra* Cogn.
Melastomataceae	*Tibouchina sellowiana* Cogn.
Monimiaceae	*Mollinedia schottiana* (Spreng.) Perkins
Myrtaceae	*Calyptranthes concinna* DC.
Myrtaceae	*Campomanesia guaviroba* (DC.) Kiaersk.
Myrtaceae	*Eugenia brasiliensis* Lam.
Myrtaceae	*Myrceugenia myrcioides* (Cambess.) O.Berg
Myrtaceae	*Myrcia anacardiifolia* Gardner
Myrtaceae	*Myrcia brasiliensis* Kiaersk.
Myrtaceae	*Myrcia palustris* DC.
Myrtaceae	*Myrcia pubipetala* Miq.
Myrtaceae	*Myrcia racemosa* (O.Berg) Kiaersk.
Ochnaceae	*Quiina glaziovii* Engl.
Rubiaceae	*Psychotria suterella* Müll.Arg.
Sabiaceae	*Meliosma sellowii* Urb.
Salicaceae	*Casearia obliqua* Spreng.
Sapotaceae	*Chrysophyllum inornatum* Mart.
Solanaceae	*Solanum diploconos* (Mart.) Bohs
Symplocaceae	*Symplocos uniflora* (Pohl) Benth.
Urticaceae	*Coussapoa microcarpa* (Schott) Rizzini